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(With the author's Compl^{ts})

5.

ON

A N O M A L U R U S,

ITS

STRUCTURE AND POSITION.

BY
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[From the PROCEEDINGS OF THE ZOOLOGICAL SOCIETY OF LONDON,
February 16, 1875.]

(Plate XXI.)

This genus was established by Mr. Waterhouse in 1842*, and now contains four or five species, all natives of Tropical Western Africa. In external appearance the Anomalures very closely resemble the larger Flying Squirrels (*Pteromys*)—their most striking outward distinctions being the double series of large salient scales on the lower surface of the first third of the tail, and the fact that the cartilage which serves to extend the flying expansion has its origin at the elbow instead of at the wrist. They are also described as

* P. Z. S. 1842, p. 124.

having similar habits, climbing lofty trees, and passing by a great sailing bound from the summit to another stem; in ascending a tree the caudal scales are pressed against the trunk and thus serve as "climbing-irons." But Mr. Waterhouse pointed out, in his original description, that the genus differs not only from the Flying Squirrels, but from all the other *Sciuridæ*, in many important characters of the skull and dentition—notably in the large size of the infraorbital opening, the almost entire absence of postorbital processes, the contraction and emargination of the bony palate, and the number and appearance of the grinding-teeth.

Since its discovery, zoologists have held very various views as to the true affinities of the Anomalure. Mr. Waterhouse regarded it as an aberrant Squirrel, showing an approach to the Dormice*. Dr. Gray took the same view, placing it at the head of the *Sciurina*, immediately following the *Myoxina*†. Temminck treated *Anomalurus* as a subgenus of *Pteromys*, and first gave some account of the skeleton‡, which was more fully described by Gervais§, and figured in the posthumous part of De Blainville's 'Ostéographie'¶. According to the views which M. Gervais then held, the subfamily *Anomalurina* had no real relationship to the Squirrels, but should be ranked among the *Hystriidæ*, next to *Capromyna*—an arrangement to which Giebel¶¶ and Burmeister** gave their adherence. Brandt first placed the Anomalures as the third tribe of his family *Sciuroides*, under the name of *Anomaluri* seu *Pteromyoxosciuri*, as indicating their relationship††, but subsequently proposed another classification, in which they formed the first subfamily, named *Anomalurini* seu *Sciuri Lemuriformes*, as showing an approach to the Lemurs, through *Galeopithecus*, in the structure of their toes and claws‡‡. M. Gervais has since withdrawn from his first position as to the hystricine affinities of the animal, but, still holding that it is not a Squirrel, unites it with the Dormice and the Miocene genera *Theridomys* and *Archæomys* in his "famille des Myoxidés"§§. In this he has been followed by Dr. Fitzinger¶¶¶. Prof. Lilljeborg placed *Anomalurina* as a subfamily of *Sciuridæ* showing an approach to the Hystricomorpha of Brandt¶¶¶; and more recently he retains this arrangement, but suggests that the form should probably rank as a distinct family***. This last view is shared by Dr. Gill, who makes the *Anomaluridæ* a family equal in value to the *Sciuridæ*, and places it between the latter and the *Haplodontidæ*†††.

* Ann. & Mag. Nat. Hist. x. p. 202 (1842).

† List Mamm. Brit. Mus. p. 133 (1843).

‡ Esquisses Zoologiques, pp. 143–146 (1853).

§ Ann. Seien. Nat. (3^e sér.) xx. pp. 238–246, pl. xiii. (1853).

¶ Atlas, iv. *Sciurus*, pl. i. (1855). ¶¶ Allgemeine Zoologie, p. 485 (1854).

** *Thiere Braziiliens*, Th. i. p. 341 (1854).

†† Mém. de l'Ac. St. Pétersb. (6^e sér.), Sc. Nat. vii. pp. 298, 299 (1855).

‡‡ Compt. Rend. Ac. Seien. xliii. pp. 139–143 (1856).

§§ Zoologie et Paléontologie Française (2^e éd.) pp. 27–30 (1859).

¶¶ Sitzungsber. Ak. Wissensch. Wien, lv. (erste Abth.) p. 511 (1867).

¶¶¶ Syst. Gefv. de Gnagando Däggdjuren, pp. 38, 40 (1866).

*** Sveriges och Norges Rygggradsdjur, i. p. 383 (1874).

††† Smithsonian Miscellaneous Collections, xi. p. 21 (1874).

Through the kindness of Professor Flower and Dr. Günther, I have been enabled to examine specimens of two species of *Anomalure* preserved in spirits in the Museum of the Royal College of Surgeons and the British Museum, and have hence been led to reconsider the question of the nature and affinities of the animal. I have to acknowledge the kind help of my friend Mr. Garrod in the examination and comparison of the very remarkable viscera, which do not appear to have been previously described.

STRUCTURE.

External characters.—With regard to these little can be added to Mr. Waterhouse's excellent original description. On examining specimens in spirits, however, one peculiarity is observed which is less striking in dry skins. This is the arrangement and form of the tubercles on the naked soles of the feet. The fore feet have a series of *five* tubercles at the base of the toes (in *A. pelii* the second inner tubercle is nearly divided in two); behind these there is a small round isolated one in the centre of the sole, and on each side a

Fig. 1.



a. Fore foot, b. Hind foot, of *Anomalurus fraseri*, natural size.

larger callosity. In the hind feet there is a series of *six* at the base of the toes, with a small central, one long internal, and two external tubercles. This remarkable arrangement, which is very similar in all the species, is well shown in the figure. The number of scales in the caudal series varies slightly in different individuals. As already noticed, the cartilage, or chondrified fascia, which supports the flying expansion or *patagium*, is attached to the olecranon instead

of to the carpus, although the membrane itself springs from the side of the wrist*. Thus instead of extending along the free front margin of the patagium as in *Pteromys* and *Sciuropterus*, it passes diagonally between its folds to the anterior corner. In the one arrangement the cartilage may be compared to the yard of a lug-sail, in the second to the gaff of a sprit-sail.

Skeleton.—The skeleton of Pcl's Anomalure having been described and figured by Gervais and De Blainville, it will be sufficient to remark on the points which bear more especially on the affinities of the animal.

The skulls of *A. fraseri*, *A. pelii*, and *A. beecrofti* are very much alike, though the examination of a series of each would probably show constant specific characters. On comparing the skull of *A. pelii* with that of *Pteromys nitidus*, the differences already alluded to are very striking. The postorbital processes of the frontals are rudimentary and almost obsolete in the Anomalure, while they are largely developed in the Flying Squirrel; on this point, however, too much weight should not be laid; for in the African Ground-Squirrels (*Xerus*) and the Chipmunks (*Tamias*) these processes are comparatively small. The other distinctions are all connected with the function of mastication. The infraorbital foramen is expanded into a large suboval opening in the anterior root of the zygoma, and evidently gives passage to a portion of the masseter muscle, as well as to the infraorbital branch of the fifth pair of nerves, instead of transmitting the nerve only as in *Pteromys* and the other *Sciuridæ*. The glenoid cavity is narrower, the articular surface of the condyle of the mandible is more sloped outwards; and the bony palate is much contracted, convex, and deeply emarginate behind.

In all other essential characters the skulls appear to me to agree. The nasals are narrower in the Anomalure (as they also are in *Xerus*), but of the same general form. The frontals are not more contracted (if the postorbital processes be disregarded), and have the same median depression. The direction of the temporal ridges is the same, as are the position of the foramina of the base of the skull, and the size of the incisive foramina. The structure of the auditory bullæ is identical, their interiors being partially divided into cells by imperfect bony septa, radiating from the walls towards the cochlea: the external meatus is large in both; but in the Anomalure its margin is less produced†. The form and proportions of the mandible are the same in both animals.

The other parts of the skeleton of the Anomalure differ in no important point from that of the Flying Squirrel, except the number of ribs, of which there are sixteen pairs instead of twelve, and the flattening and breadth of the olecranon, to give attachment to the cartilage of the flying expansion. The vertebræ of *A. pelii* are:—

* Temminck was therefore mistaken in stating that the forearm is free in the Anomalure (Esquiss. Zool. p. 145).

† Since the above was written, my friend Mr. A. Doran has called my attention to the auditory ossicles of *Anomalurus*, which are identical in type with those of the true Squirrels.

cervical 7, dorsal 16, lumbar 9, sacral 4, caudal 28; the latter are much elongated. The posterior ridge of the scapula is very salient; and the humerus has a moderate deltoid ridge. The femur has a crest representing the third trochanter; and the slender fibula is quite distinct from the tibia; in *Pteromys* these bones are often closely united below, though not truly fused.

Dentition.—The grinding-teeth of the Anomalure are four in number on each side above and below, the small anterior premolar of *Pteromys* being absent; this tooth, however, is lost early in life in many species of Squirrel. Their series converge in front; and they are placed obliquely; so that the crowns of the upper teeth look outwards, and those of the lower jaw inwards. These crowns are worn perfectly flat even in young individuals, exposing islands of cement separated by cross folds of enamel, which are more directly transverse and less twisted than in the more complicated teeth of *Pteromys*. In the typical skull of *A. beecrofti*, in the British Museum, the cemental spaces are smaller and more isolated than in the other species.

Viscera.—These, like the masticatory apparatus, differ much from those of the *Sciuridae*, and, indeed, present peculiarities not met with in any other family of the order.

Fig. 2.



Caecum of *A. fraseri*, natural size.

The tongue resembles that of the Squirrels, but is narrower and more pointed. The circumvallate papillæ are two in number, and are placed transversely.

The œsophagus has a short abdominal course after passing through the diaphragm, extending in *A. fraseri* to about half an inch; its epithelium is not continued beyond the cardiac orifice.

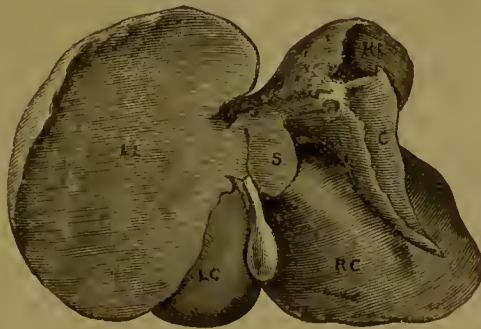
The stomach is perfectly simple and nearly oval, the cardiac and pyloric openings being near one another. The walls are very thin; and the epithelial lining is smooth and perfectly uniform throughout. A very small external fold or pucker runs transversely across the lesser curvature. In *A. fraseri* the greatest diameter is 1·75 inch, the lesser about ·80.

The duodenum has the usual dilatation below the pylorus; the length of the small intestine in *A. fraseri* is 43·50 inches, and in *A. pelii* 60 inches.

The cæcum is of considerable volume. In *A. fraseri* its length is about 5 inches, and its greatest diameter ·50; in the specimen examined of *A. pelii* its proportions were similar, but it was too greatly injured by shot to allow of exact measurement. In form and structure it is very different from that of the Squirrels, and, indeed, from that of any of the *Glires Simplicidentati* with which I am acquainted. It is at first continuous with the colon, irregularly coiled on itself, and sacculated almost to its end by an internal spiral fold, with a free inner edge, as in the Hares; this fold is nearly regular and continuous, but here and there it is interrupted. The extremity is very narrow, perfectly simple, and abruptly reflected on itself. In the figure the cæcum is shown uncoiled and extended, in which condition its structure is more plainly shown than when it is in its natural convolutions.

The colon is at first marked by the inner fold continued from the cæcum; its first loop after leaving the latter is longer than the second. The length of the large intestine from cæcum to anus is in *A. fraseri* about 16 inches, in *A. pelii* 47 inches, making the whole length of the intestine about 60 inches in the former and 107 inches in the latter, or rather more than *five* times the length of the head and body in each case.

Fig. 3.



Liver of *A. fraseri*, natural size.

LL, left lateral lobe; LC, left central; RL, right lateral; RC, right central;
S, Spigelian; C, caudate lobe.

The spleen is of the same shape as in the Squirrels.

The liver has the general proportions shown in the figure. The caudate lobe is long and pointed; it is proportionally smaller in *A. pelii* than in *A. fraseri*. The Spigelian lobe is small and simple, not double or bifid as in almost all known rodents. There is no trace of a cystic notch; and the gall-bladder lies directly over the umbilical fissure—an arrangement which has never been observed, as far as I know, in any other member of the order.

The uterus of the female is long and double. In the male the penis is stated by Gervais to be provided with a bone.

SYSTEMATIC POSITION.

From the above facts it appears to be clear that the Anomalure is an aberrant Squirrel, with no special affinities to any other family, that its peculiarities are all purely adaptive, and that they are all in direct connexion with the functions of mastication and digestion.

Thus, in the skull, if we pass the minor point of the reduction of the postorbital processes, we find that it is built on the true sciurine type, *except* in those parts which are modified by the peculiarities of the masseter muscle and teeth. Mr. Waterhouse, with his usual acumen, remarked in his original description:—"The masticating surfaces of these teeth are worn flat by usage, even in the comparatively young animal, as in other rodents which have a large ant-orbital opening, and have not a tubercular surface such as we find in the molars of the typical Squirrels. These last-mentioned animals, it would appear, have a rotatory motion of the lower jaw, while the *Anomaluri* have a longitudinal, no doubt combined with the rotatory motion; and this difference is perhaps due to the action of that portion of the masseter muscle which passes through the antorbital opening" (*l. c.* p. 127)*. The rest of the skeleton, save in the number of ribs, seems also to be that of a true Squirrel; and though the viscera are widely different from those of that group, yet they are also unlike the organs of any other family.

The resemblances which have been pointed out to the Dormice and to the hystricine rodents appear to me to be merely superficial and adaptive. Those to the *Myoxidæ* are only in the size (not the form) of the infraorbital opening, and the number and general appearance of the grinding-teeth, and do not extend to any more important characters. The points of similarity to some of the *Hystricidæ*, in the form of the infraorbital opening, the shape of the bony palate, and the number of ribs, are much more striking, but are at once negatived by the structure of other parts, notably by that of the mandible, zygoma, auditory bullæ, and base of the skull. The teeth, which M. Gervais compares to those of *Cercomys*, have not so great a resemblance to the teeth of any of the *Hystricidæ* as the dentition of the Beaver has to that of the widely distinct Coypu. Brandt's comparison of *Anomalurus* to

* Cf. Von Teutleben, Archiv f. Naturgeschichte, 1874, pp. 91-93.

Galeopithecus, founded on the compression of the toes and claws, seems too fanciful to require discussion, though by a curious coincidence the cæca of the two animals are somewhat similar in appearance.

What may have been the causes of the wonderful modification of the alimentary system and the subsidiary parts of the skull in *Anomalurus* is more doubtful. The facts seem to point to the effect of a more dry and innutritious diet. Beyond Temminck's statement that "ils se nourrissent de fruits," nothing has been recorded of the food of the Anomalures; and the contents of the stomachs of the specimens I have examined were unfortunately too well digested to yield much information. That of *A. pelii*, however, contained a quantity of long vegetable fibres, which seems not unfavourable to the idea that they may live principally either on dry and stringy fruit or on leaves.

A further question, and one perhaps incapable of a satisfactory solution, remains. Is *Anomalurus* more closely allied to *Pteromys* and *Sciuropterus* than to the non-volant genera of the family? or are their resemblances an instance of the independent origin of similar structures? The development of a flying-expansion in itself naturally points to the former view, while the remarkable difference in the attachment and course of its expanding cartilage seems to be in favour of the latter.

The geographical distribution of the two groups is worthy of note. As far as we know at present, the Anomalures appear to be confined to a limited region of West Africa, extending from the equator to about 15° north latitude, whereas no species either of *Pteromys* or *Sciuropterus* seems ever to have been met with in any part of the Ethiopian region.

If the above views are correct the systematic position of the Anomalures is settled, and their rank will merely depend on the higher or lower value given to the whole sciurine group of rodents. If the latter is regarded as a family, then the *Anomalurinae* will be a subfamily of *Sciuridae*; if as a separate section of the order, the *Anomaluridae* will form one of the constituent families of the *Sciuromorpha*. In either case the characters will be the same as those proposed by Mr. Waterhouse for the only known genus.

I now conclude with the synonymy, characters, and habitats of the known species of the genus.

SPECIES.

1. ANOMALURUS FRASERI.

1842. *Anomalurus fraseri*, Waterhouse, P. Z. S. 1842, p. 124; Ann. & Mag. Nat. Hist. x. p. 201.

1842. *Pteromys derbianus*, Gray, Ann. & Mag. Nat. Hist. x. p. 262.

1843. *Anomulurus derbianus*, Gray, List Mamm. Brit. Mus. p. 133.

1860. *Anomalurus beldeni*, Du Chaillu, Proc. Boston Soc. Nat. Hist. vii. p. 303*.

Above grizzled sooty brown, extremities darker, area round ears blackish. Below dirty white, chin and throat dark grey. Measurements of a small specimen in the flesh:—head and body 11 in., tail 11.50, ear 1.30, fore foot (without claw) 1.40, hind foot 2.

Hab. Fernando Po (*Fraser, Brit. Mus.*); Gambia? (*Brit. Mus.*); Ashantee (*Mus. R. Coll. Surg.*).

2. ANOMALURUS PELII.

1845. *Anomalurus pelii*, Temminck, Verhand. over de Nat. Geschied. der Nederl. Bezitt. i. (d. ii.) p. 108; Esquisses Zool. (1853), p. 146.

Above sooty black; the broad margin of the flying-expansion, nose, long hairs at base of ears, tail, and lower parts white; feet white, mixed with dusky. Measurements of a specimen in the flesh:—head and body 17 in., tail 17.75, ear 1.75, fore foot 1.60, hind foot 2.50.

Hab. Fantee, Ashantee (*Pel, Leyden Mus.*; *Brit. Mus.*).

3. ANOMALURUS BEECROFTI.

1852. *Anomalurus beecrofti*, Fraser, P. Z. S. 1852, p. 17, pl. xxxii.

Above grizzled yellowish grey, washed along the spine with rufous; front part of flying-expansion dusky; a short pale band on each side of the neck, and a small white spot between the ears; tail dusky brown. Below bright rufous. Measurements of a dry skin:—head and body 15 in., tail 9.

Hab. Ashantee (*Fraser, Brit. Mus.*); Cameroon Mountains, 7000 feet above sea (*Burton, Brit. Mus.*)†.

4. ? ANOMALURUS LANIGER.

1853. *Anomalurus laniger*, Temminck, Esquisses Zoologiques, p. 149.

Above grizzled grey, washed along the spine and on the shoulders with rufous; tail brown. Throat and breast rufous, rest of the lower parts reddish white. Fur throughout short, thick, woolly, and crisp. Measurements of a dry skin:—head and body 9 in., tail 7.

Hab. West Africa, exact locality not known (*Leyden Mus.*).

I have not seen Temminck's type, which is described as not fully grown and in bad condition. Probably it is the young of the last species, in which the fur is certainly shorter and more woolly than in the others.

5. ANOMALURUS FULGENS. (Plate XXI.)

1867. *Anomalurus fulgens*, Gray, Ann. & Mag. Nat. Hist. (4th ser.), iii. p. 469.

Nearly uniform bright rufous, rather paler below, and passing to

* Cf. Gray, P. Z. S. 1861, p. 275.

† Cf. P. Z. S. 1862, p. 180.

whitish on the sides of the abdomen ; a small white spot between the ears. Measurements of a dried skin :—head and body 14 in., tail 7.

Hab. Gaboon (*Brit. Mus.*).

As far as I am aware, the type specimen of this very handsome species is still the only one which has been brought to Europe ; and as it has not hitherto been figured, I have chosen it as the subject of the accompanying plate.

